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THE DISTRIBUTION OF DWARF MISTLETOES, ARCEUTHOBIUM, IN CALIFORNIA

JOB KUIJT

There has long been need of a more careful geographical study of the western dwarf mistletoes than has been available thus far. This paper attempts, first of all, to correct certain misconceptions which have been carried along in the relevant literature. Secondly, it represents an effort to bring up to date what is reliably known about the distribution of dwarf mistletoes in California. Finally, it tries to discover whether there is geographical evidence for the existence of host forms in *Arceuthobium campylopodum* Engelm.

The California distribution of dwarf mistletoes is indeed of crucial importance in geographical considerations in the genus as a whole. For it is in this state that the Pinaceae, a family embracing all known hosts of North American dwarf mistletoes, reaches a high level of diversity. The geographic peculiarities of the genus in California may thus contribute

to the understanding of similar features elsewhere.

The lists and maps contain all Californian collections of A. americanum Nutt, ex Engelm, and A. douglasii Engelm, which I have been able to find in the herbaria of the University of California at Berkeley and Los Angeles (UC and LA, respectively), the California Academy of Sciences at San Francisco (CAS), the Dudley Herbarium of Stanford University (DS), the two herbaria at Claremont (POM and RSA), the Santa Barbara Museum of Natural History (SBM), and the United States Department of Agriculture Forest Pathology herbaria at Albuquerque (FPA) and Berkeley (FPB). Such an approach is at this time not feasible for A. campylopodum, as hundreds of collections of this species have been made in California. I have chosen instead to select a number of collections of this species to be recorded here. This selection has been carried out with two objectives in mind: firstly, to give as extensive a picture of the distribution of A. campylopodum in the state as possible; and secondly, to compare the geographic ranges of the supposed host forms of this species. Such a procedure does not give a reliable idea of frequency of occurrence. This would have been equally true, however, had all collections been taken into account, because some recreational areas are represented in herbaria by disproportionally large numbers of collections. This is true particularly for the Monterey Peninsula. In a similar way, the mistletoe on digger pine is much more accessible and much more in evidence than, for example, the same species on sugar pine, and therefore the former is present in herbaria in numbers exaggerating its relative frequency. I believe therefore that selection of specimens, when based on some acquaintance with the species as they occur in nature, in this way can give a somewhat more accurate idea of geographic distribution. I am also refraining from citing specimens

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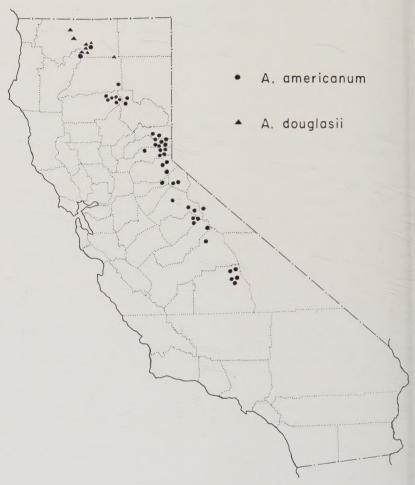


Fig. 1. Distribution of Arceuthobium americanum and A. douglasii in California.

which I have not personally seen. Especially in Gill (1935) some additional citations may be found which do not, however, modify the distributional patterns as here described, except where this author has repeated erroneous records from previous publications.

ARCEUTHOBIUM AMERICANUM Nutt. ex Engelm.

The lodgepole pine mistletoe is known from the boreal forests of the four western Canadian provinces and from all states west of the Rocky Mountains. It has been collected from a number of pines as well as from *Picea glauca* (Moench) Voss (Kuijt, 1955), but in California it is known from only *Pinus contorta*, *P. ponderosa*, and *P. jeffreyi* (see map, fig. 1).

On Pinus contorta Dougl. ex Loud.

TULARE COUNTY. North fork of Kern River, 2150 m., Coville & Funston 1596 (DS); Bakeoven Meadows, 8100 ft., Howell 27038 (CAS, DS, UC); ridge between Monache Meadows and Bakeoven Meadows, 8200 ft., Munz 15220 (RSA); Funston Camp, Kern River Canyon, 6700 ft., Peirson 1720 (RSA); Junction Meadows, Kern River, 8000 ft., Raven 8349 (CAS, UC). Fresno County. Huntington Lake, 7000 ft., Solbrig 2420 (UC). MADERA COUNTY. Red's Meadows to Rainbow Falls, 7100 ft., Raven 3678 (CAS, RSA). MARIPOSA COUNTY. Merced Lake trail, Yosemite National Park, Schreiber 1948 (UC); Little Vosemite Valley, Bolander 5095 (UC), Rodin 877 (UC). TUOLUMNE COUNTY. Glen Aulin Camp, Baldauf (CAS); Morrison Creek, Mount Adams, Braekett (LA); YMCA camp, Pinecrest, 5500 ft., Gill (FPA). Mono COUNTY. 4.3 mi. west of Highway 120-395 junction, Kuijt 1390 (UC). ALPINE COUNTY. Camp Wolfeboro, Kuijt 1411 (UC); 0.5 mi. east of Grade Summit, Kuijt 1412 (UC). AMADOR COUNTY. East of Lower Bear River Reservoir, Ouick 54-88 (CAS). EL DORADO COUNTY. Near Lily Lake, Glen Alpine Canyon, Abrams 12753 (DS, RSA, UC); 16 mi. south of Tahoe City, Kuijt 1335 (UC); Highway 50 at Pyramid Creek, Kuijt 1513 (UC). PLACER COUNTY. 8.5 mi. west of Soda Springs, Kuijt 1330 (UC); 10 mi. north of Tahoe City on Highway 89, Kuijt 1331 (UC); 3.5 mi. north of Tahoe City on Highway 89, Kuijt 1332 (UC); Tahoe Meadow, Schreiber 776 (UC). NEVADA COUNTY. Near Donner Lake, Dudley (DS); Mayen's Meadow, near Truckee, Sonne (UC); Trout Creek near Truckee, Thomson (CAS); Truckee, 6300 ft. (FPA); Hobart Mills (FPA). SIERRA COUNTY. 9.5 mi. north of Truckee, Kuijt 1344 (UC); Salmon Lake, Sutliffe (CAS); Gold Lake (FPA). Plumas COUNTY. 18 mi. north of Greenville on Highway 89, Kuijt 1350 (UC); Gold Lake, Mason 1079 (UC). TEHAMA COUNTY. 7 mi. west of Highway 36-89 junction at Lake Almanor, Kuijt 1352 (UC); 13 mi. west of Highway 36-89 junction at Lake Almanor, Kuijt 1354 (UC); near Ranger Station, Mineral Campgrounds, Kuijt 1358 (UC); along Deer Creek, 1.5 mi. south of Highway 32-36 junction, Kuijt 1501 (UC); Spring camp near Childs Meadow, Quick 53-129 (CAS). SHASTA COUNTY. Thousand Lake Basin, 6400 ft., Peirson 10136 (RSA). SISKIYOU COUNTY. Military Pass, Mount Shasta, Cooke 16034 (DS, UC); north fork, Sacramento River, 6600 ft., Raven 10456 (CAS).

On Pinus ieffrevi Grev. & Balf.

PLACER COUNTY. 9.2 mi. north of Tahoe City on Highway 89, Kuijt 1343 (UC).

On Pinus ponderosa Dougl. ex Laws.

Tehama County. 13 mi. west of Highway 36-89 junction at Lake Almanor, Kuijt 1355 (UC).

DISCUSSION. California represents one of the two southernmost extensions of the lodgepole pine mistletoe, the other being in the Rocky Mountain area of Colorado. From a comparison of Figure 1 with the known distribution of *Pinus contorta* (Critchfield, 1957, fig. 26), it is evident that at least in California the geographic range of the lodgepole pine mistletoe corresponds rather closely to that of its most common host. The exceptions to this rule are seen in the isolated and apparently healthy populations of lodgepole pine in the San Bernardino and San Jacinto mountains, California, and in Baja California, Mexico, and of *P. contorta* subsp. *bolanderi* (Parl.) Critchf. on the Mendocino coast of California. It is also notable that the subsp. *contorta*, although in direct contact with subsp. *murrayana* (Balf.) Critchf. in northern California, has not yet been reported as host for *Arceuthobium americanum*. Indeed this appears

to be true outside the state, as I have seen no record of A. americanum anywhere in the range of Pinus contorta subsp. contorta (Kuijt, 1956). This is more likely to be a case of ecological or spatial isolation than resistance on the part of the host, as various other species of pine and even a spruce may be parasitized by Arceuthobium americanum. Furthermore, all subspecies of Pinus contorta are susceptible to Arceuthobium campylopodum in one or more localities.

It is a remarkable fact that A. americanum appears to be unable to perpetuate itself for long periods of time in stands of Pinus jeffreyi and P. ponderosa. Wherever infected individuals of these hosts are found, infected lodgepole pine is nearby and almost surely is the source of the former infections. This is the more remarkable because the brooming induced on Jeffrey and ponderosa pine is almost identical to that on lodgepole pine (Kuijt, 1958). There are factors quite apart from symptomatology, therefore, which distinguish the spread of this species of dwarf mistletoe in stands of various pine species. Whether these factors are climatological, or whether in Jeffrey and ponderosa pine there is a greater percentage of resistant trees, is impossible to say at present.

ARCEUTHOBIUM CAMPYLOPODUM Engelm.

This species is the most abundant one in California (see map, fig. 2). Outside the state it is found from Alaska and British Columbia, largely west of the Rocky Mountains, to the Mexican border (and across into Baja California). It parasitizes species of *Abies, Larix, Pinus, Picea*, and *Tsuga*. All but *Larix* have been reported as hosts for *Arceuthobium campylopodum* in California, but in greatly different frequencies.

I have attempted, both in the listing and mapping of the specimens selected for my purpose, to group herbarium specimens according to the affinities of their hosts. In this way I have used the following host categories as criteria for division: *Abies*; *Picea*; *Tsuga*; and the three main subdivisions of *Pinus*, namely, the yellow, white, and pinyon pines. I want to make clear that such a subdivision is not based on my acceptance of the corresponding host forms as recognized by Gill (1935), but rather is an effort to test their validity.

On Abies.

Tulare County. Cone Peak Camp, Kaweah and Kings River, Dudley (DS); between Junction Meadows and the hot springs, 7500 ft., Raven 8381 (CAS). Fresno County. Charlotte Creek, Bubbs Creek, Howell 15674 (CAS); 2 mi. south of summit of Shaver Lake-Dinkey Creek road, Quick 53-27 (CAS); Huntington Lake, 7000 ft., Wall 67 (CAS). Tuolumne County. Southeast of Strawberry Lake, 6500-7200 ft., Quick 1734 (CAS); southeast of Pinecrest, Quick 50-40 (CAS); Tuolumne Canyon, Clemens (CAS). Amador County. East of Lower Bear Reservoir, Quick 54-87 (CAS). Alpine County. Silver Creek, east side of Ebbetts Pass, 6800 ft., Howitt (CAS). El Dorado County. Near north end of Echo Lake, Howell 22902 (CAS); near Camino, Kuijt 1272 (UC); Tehoma, Lake Tahoe, Kuijt 1340 (UC). Placer County. Trail to Mount Ellis above Homewood, Schreiber 891 (UC). Nevada County. Baltic Trail, Dudley (DS). Plumas County. Taylorsville, Clements (CAS); 8 mi. north of Greenville, Kuijt 1349 (UC). Butte County. Jonesville, 1600 m.,

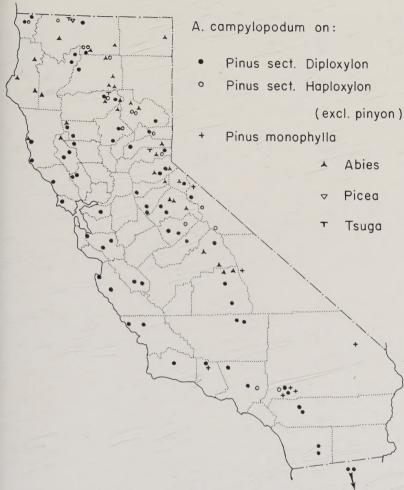


Fig. 2. Distribution of Arceuthobium campylopodum in California.

Copeland (CAS). Tehama County. 11 mi. west of Highway 36–89 junction at Lake Almanor, Kuijt 1353 (UC); 5 mi. west of Mineral, Kuijt 1359 (UC). Shasta County. Highway 89 at Pondosa junction, Kuijt 1368 (UC); 1.5 mi. east of Viola, Kuijt 1364 (UC). Lassen County. 1 mi. below Drakesbad, Mount Lassen, 5400 ft., Cain 114 (DS); Crater Mountain, ca. 15 mi. west of Eagle Lake, 7300 ft., Whitney 1703 (UC); Modoc County. Campgrounds at Cedar Pass, Warner Mountains, Alava (UC). Siskiyou County. East of Bartle, at border of Modoc National Forest, Newcomb 156 (UC); Sisson southern trail, Mount Shasta, Cooke 13574 (DS); summit of Cayenne Ridge, near Marble Mountain, Ownbey 2212 (CAS, DS). Humboldt County. Lasseck's Peaks, between Goat Camp and Signal Peak, Kildale 2634 (DS); ridges east of Corral Prairie, Trinity Summit, Tracy 10571 (UC); Eureka, Tracy 3984 (UC). Trinity County. South Fork Mountain, Parks & Tracy (UC). Mendocino County. Van Damme State Park, Kuijt 1216 (UC). Glenn County. Plaskett Meadows, 6000 ft., Howell 19283 (CAS). Lake County. Mackie (UC): see the discussion under A. douglasii.

On Picea breweriana Wats.

Siskiyou County. Ridge above Applegate Creek, Dry Lake Lookout, 6500 ft., Meinecke (FPB).

On Tsuga mertensiana (Bong.) Carr.

PLACER COUNTY. Emigrant Gap, Jones (POM). TEHAMA COUNTY. Mineral, 6300 ft., Long (FPB). SISKIYOU COUNTY. Along head of Applegate Creek, north side of pass to Fort Gough, 6000 ft., Meinecke (FPB).

On Yellow Pines. (Pinus sect. Diploxylon: P. attenuata Lemmon, P. contorta, P. jeffreyi, P. ponderosa, P. coulteri Don, P. sabiniana Dougl. ex

Don, P. radiata Don, P. muricata Don.)

BAJA CALIFORNIA, MEXICO: Low hills northwest of La Encantada, Sierra San Pedro Mártir, 7300-7400 ft., Wiggins & Demaree 5018 (DS, UC, LA); "San Pedro Martir", Brandegee (UC). CALIFORNIA: SAN DIEGO COUNTY. Pine Hills, near Julian, ca. 4250 ft., Brown (RSA); base of Stonewall Peak, Wiggins 2725 (DS). RIVERSIDE COUNTY. Idyllwild-Banning, Clokey & Anderson 6574 (RSA, UC); south side of San Jacinto Mountains, 5400 ft., Hall 2616 (UC). SAN BERNARDINO COUNTY. Mill Creek, Smith 15A (UC); Lake Arrowhead, MacFadden 14737 (CAS). Los An-GELES COUNTY. Elizabeth Lake Canyon, Liebre Mountains, Dudley & Lamb 4411 (DS); Pine Flats, 20 mi. north of Sierra Madre, Angeles N.F., 6000 ft., Sloan (FPB). VENTURA COUNTY. Mount Pinos, Hall 6642 (UC). SANTA BABRARA COUNTY. Figueroa Mountain, Pollard (CAS). KERN COUNTY. Near Havilah, 900 m., Coville & Funston 1073 (DS); 4 mi. west of Kernville, 4000 ft., Gould 1010 (DS). SAN LUIS OBISPO COUNTY. Cambria, Hoover 6448 (CAS); Santa Margarita, Mason 525 (UC); near Paso Robles, Summers 926 (UC). TULARE COUNTY. Near Mineral King, 2700 m., Coville & Funston 1460 (DS); Peppermint Valley, Dudley (DS). Fresno County. Vermillion Valley, 7700 ft., Raven 5825 (CAS). SAN BENITO COUNTY. On ridge above New Idria reservoir, Kuijt 1310 (UC); on road to New Idria, 4.5 mi. south of Bitterwater junction, Kuijt 1300 (UC). Monterey County. Pacific Grove, Coleman (DS); Millers Canyon, Santa Lucia Mountains, 4300 ft., Ferris 12158 (DS). SANTA CLARA COUNTY. Loma Prieta, Dudley (DS); slopes of Mount Umunhun, Ferris 2083 (DS); Arboretum, Stanford University, Long (DS).2 Contra Costa County. Mount Diablo, Abrams 4356 (DS). MADERA COUNTY. Ca. 9 mi. west of Oakhurst, Kuijt 1254 (UC). Mariposa County. Ca. 3 mi. west of Mount Bullion, Kuijt 1253 (UC); on road to Wawona, Jussell 13 (UC), Tuolumne County, Cottonwood Meadows, east of Mather, Clausen 1777 (DS); near Pinecrest, Quick 55-46 (CAS). CALAVERAS County. West of Stanislaus River on road from Vallecito to Columbia, Quick 53-141 (CAS); 1.5 mi. east of Copperopolis on Highway 4, Kuijt 1410 (UC). AMADOR County. On road to Buena Vista, ca. 1 mi. south of Ione, 400 ft., Newcomb (UC). Mono County. 3 mi. east of Sonora Pass, Kuijt 1432 (UC). ALPINE COUNTY. Silver Creek Public Camp, Munz 21347 (RSA). EL DORADO COUNTY. Lily Lake, Glen Alpine Canyon, Abrams 12752 (DS); near Camino, Kuijt 1273 (UC). PLACER COUNTY. 1 mi. north of Tahoe City on Highway 89, Kuijt 1333 (UC). NEVADA COUNTY. Spenceville, Eastwood 3420 (CAS). SIERRA COUNTY. Gold Lake, Barker 254 (DS). BUTTE COUNTY. Hills near Big Chico Creek, east of Chico, Heller 11144 (DS); Bangor, Rose (CAS). Plumas County. 21.5 mi. north of Sierraville, Kuijt 1346 (UC). Shasta COUNTY. Near Morleys, Baker (UC). SISKIYOU COUNTY. Sisson southern trail, Mount Shasta, Cooke 11593 (CAS, DS, UC); west of Craggy Mountain, northwest of Yreka,

Introduced into the Arboretum at an early date, since the mistletoe was already

there at the turn of the century (Peirce, 1905).

¹ As far as I can ascertain, these are the only Mexican records of A. campylopodum. The species A. vaginatum, which is not known from California or Baja California, does occur in areas of non-peninsular Mexico.

Ownbey & Brown 2425 (UC). Del Norte County. Gasquet Mountain, Eastwood 12138 (CAS); Elk Camp Ridge, Parks 24063 (UC). Trinity County. Near Scott Ranch, Cantelow 1659 (RSA); near Trinity Center, Howell 12790 (CAS). Tehama County. 15 mi. west of Highway 36–89 junction at Lake Almanor, Kuijt 1357 (UC); Manton, Kuijt 1362 (UC). Mendocino County. Pygmy forest above Van Damme State Park, Kuijt 1215 (UC); Point Arena, Mason 7168 (UC). Glenn County. 5 mi. above Long Point Fire Lookout Station, 3750 ft., Newcomb 148 (UC); 2.1 mi. north of Stonyford, Kuijt 1506 (UC). Lake County. Kelseyville, Jussell (CAS); near Lucerne, Sutliffe (CAS). Colusa County. Stonyford-Upper Lake road, below Old Mill Campgrounds, 3700 ft., Newcomb 146 (UC). Napa County. Mount St. Helena, Howell 2204 (CAS); 3 mi. from Aetna Springs on Butts Canyon Road to Middletown, Howell 5618 (CAS). Sonoma County. Fort Ross, Mason 4285 (UC). Marin County. Inverness Ridge, Howell 19686 (CAS).

On Pinus monophylla Torr. & Frém.

San Bernardino County. East slope of Providence Mountains, Munz, Johnston & Harwood 4272 (POM); north slope of San Bernardino Mountains, Parish & Parish 1442 (DS, UC); Arrastre Creek, 3 mi. southeast of Baldwin Lake, 6700 ft., Jaeger (POM); 5 mi. southeast of Ivanpah, Gill & Wright (DS). Ventura County. Seymour Creek, Mount Pinos, 6000 ft., Peirson 3251 (POM, RSA). Inyo County. Ca. 3 mi. west of Lone Pine on Mount Whitney road, Kuijt 1389 (UC). Mono County. 6 mi. south of Coleville, Kuijt 1413 (UC).

On white pines, excluding pinyon (*Pinus* sect. *Haploxylon*, excl. pinyon: *P. albicaulis* Engelm., *P. lambertiana* Dougl., *P. flexilis* James, and *P. monticola* Dougl. ex Don).

SAN BERNARDINO COUNTY. West slope, Job's Peak, 5000 ft., on P. lambertiana, Ewan 3564 (POM, DS, UC). Los Angeles County. Between Wrightwood and Kratka Ridge, Angeles N. F., on P. lambertiana, Embree (UC). Mariposa County. Fish Camp Creek, on P. lambertiana, Hedgecock and Meinecke (UC). Mono County. On saddle above Convict Lake, 8800 ft., on P. flexilis, Kuijt 1415 (UC); 2 mi. southeast of Lundy Lake, on P. (?) flexilis, Hendrix 616 (UC). Placer County. Near Summit, Tahoe N. F., 7500 ft., on P. monticola, Wagener (FPB). SIERRA COUNTY. Between Downieville and Forest, 5000 ft., on P. lambertiana, Boyce (FPB). BUTTE COUNTY. Big Bar Mountain ridge east of Pulga, on P. lambertiana, Quick 53-32. PLUMAS COUNTY. Southeast of Meadow Valley, on P. lambertiana, Quick 53-120 (CAS); Meadow Valley, on P. lambertiana, Weatherby 1667 (UC). TEHAMA COUNTY. 2 mi. north of Hole-in-Ground Campgrounds, on P. lambertiana, Kuijt 1502 (UC). SHASTA COUNTY. Highway 89 at Pondosa junction, on P. lambertiana, Kuijt 1369 (UC). SISKIYOU COUNTY. North slope of Shastina, on P. albicaulis, Cooke 11576 (DS); west fork of Molly Creek, on P. albicaulis, Butler 272 (UC); head of Applegate Creek, 5800 ft., Wagener (FPB). DEL NORTE COUNTY. Gordon Mountain, 4100 ft., on P. monticola, Newcomb 165 (UC).

DISCUSSION. All major areas of yellow pine in California are infected by A. campylopodum. This conclusion cannot be avoided when the specimens cited above are considered. There are, however, differences in the frequency of A. campylopodum which are not evident from this enumeration. Such differences are difficult to measure, but are nevertheless recognizable in the field.

The only California yellow pine which appears to be free of this mistletoe is *P. torreyana* Parry ex Carr. I have searched for the parasite in the Del Mar area without success, and I have never seen a herbarium specimen with this pine as host. The spatial isolation of this pine from its fellow species would lead one to conclude that its health is not a question of immunity, but rather that isolation from other pines has, at the same time, kept *Arceuthobium* from reaching the Torrey pine.³ I am currently germinating *A. campylopodum* on some seedlings of this pine, but cannot as yet

report on it.4

Infected white pines have been collected a great deal less frequently than yellow pines. This is of course partly due to their comparative rarity in the state, especially *P. albicaulis*, *P. flexilis*, and *P. monticola*. *Pinus balfouriana* Grev. & Balf. has also been reported as host from Black Butte, Siskiyou County (Gill, 1935). The latter author also makes reference to a supposed host record of California *P. aristata* Engelm. by Garrett (1921) which, however, is erroneous, as Garrett reports this host only from Bryce Canyon, Utah.

The sugar pine I believe is more frequently infected than the record indicates, and this discrepancy is probably due to the inaccessibility of infections on this tree. It is nevertheless true, as Gill (1935) pointed out, that infected trees of this pine are fairly infrequent and are usually assoated with other infected members of the Pinaceae.

The pinyon pines have an even more spotty collection record. This situation indeed is evident in the field since infected trees are rare and appear to occur in small groups. The interesting fact is that such a small number of collections (these are all the pinyon records I have found from California) should be so widely spaced. I have heard it said that the pinyon pine mistletoe is equally spotty in its occurrence outside California.

As far as *Abies* is concerned, it seems to be fairly commonly infected in northern California. The incomplete record for some counties in the Sierra Nevada I suspect to be due to an infrequency of collecting rather than to a rarity of occurrence. This can be checked only by further collections, however. The notable fact in this host genus is that the geographically most isolated fir, *Abies bracteata* (Don) Poit., is free of dwarf mistletoe. Do we here have a parallel to the situation seen in *Pinus torreyana*? Is the lack of infection of *Abies bracteata* due to immunity, or to isolation from dwarf mistletoe? Cross-inoculations may well supply the answer to this question. It is an interesting fact that within a few miles of the *Abies bracteata* populations in the Santa Lucia Mountains the Coulter pine is heavily infected with *Arceuthobium campylopodum*.

There remain to be considered, finally, the only California records known of A. campylopodum on Picea and Tsuga. The small number of

 $^{^3\,\}mathrm{Dr},\mathrm{H.\,L.}$ Mason reports that the pines of Santa Cruz Island are apparently free of mistletoe.

⁴ Since writing the above, the inoculations have been inspected and found successful. The source of the mistletoe seed was Mount Diablo where the dwarf mistletoe grows indiscriminately on both *Pinus coulteri* and *P. sabiniana*. Seeds were placed individually in axils of leaves and fascicles of seedlings of *P. torreyana* (from Del Mar) less than a year of age, on November 6, 1957. At present (January, 1960) a large number of mistletoe shoots are present and one pine has died, perhaps as a result of heavy infection.

collections of these conifers as hosts, and the distances between their localities of origin, would certainly militate against basing host forms upon these genera. The three isolated collections on Mountain Hemlock are significant in this respect, but the infected *Picea breweriana* in Siskiyou County is an even better case in point. According to Gill (1935), the nearest known infected spruces are from Idaho and Arizona!

How then does the geographical evidence bear upon the status of the host forms of Arceuthobium campylopodum? It is quite clear that it does not, in itself, support the notion. The host forms considered by Gill as "minor" forms [f. cyanocarpum (Nelson) Gill, f. blumeri (Nelson) Gill, and f. microcarpum (Englm.) Gill] are found within the areas occupied by even a single "major" form, f. campylopodum. In fact, f. campylopodum is known from practically every county where any of the other forms have been collected. Gill admits that his three "minor" forms are found only in association with other infected species. In California, at least, the host forms do not have geographic independence. These facts alone, of course, do not preclude racial differentiation as to hosts.

It is a common field experience to find a heavily infected species of one tree together with another species, apparently healthy here, but infected elsewhere. This puzzling situation is frequently observed in mixed fir and pine stands of the Sierra Nevada and elsewhere. It seems to me that such situations more than any other considerations have led to the supposition of host forms. In my opinion the taxonomic recognition of such host forms ignores two important possibilities. First of all, it fails to take into account a possible variation in susceptibility even within a host species. Secondly, it largely ignores those isolated but significant instances where, for example, a lodgepole pine has become infected obviously from the heavily infected fir towering above it. When geographic data are thus considered together with the results of the past cross-inoculations (Weir, 1918) and natural apparent transfers between Pinus, Picea, Abies, Larix, and Tsuga (Kuiit, 1955) it becomes evident that the host forms are not natural groups and are, indeed, misleading. The species A. campylopodum cannot, in my opinion, be subdivided into natural groups until more is known about the resistance differences (if any) both between and within host species.

ARCEUTHOBIUM DOUGLASII Engelm.

The Douglas fir mistletoe is the rarest of California dwarf mistletoes (see map, fig. 1). Its range outside the state shows similarities to that of A. americanum. It is found from southern British Columbia to California and Arizona and New Mexico. It is not known from the coastal areas of the Pacific Northwest, even where the Douglas fir reaches its maximum development. It rarely grows on anything but Douglas fir (Pseudotsuga menziesii), the only known host from California.

On Pseudotsuga menziesii (Mirb.) Franco.

SHASTA COUNTY. Highway 89 at Pondosa junction, 4000 ft., Kuijt 1367 (UC). SISKIYOU COUNTY. Southwest slopes of Mount Shasta, 5000 ft., Cooke 13920 (LA);

north side of Cascade Gulch, Mount Shasta, 5000 ft., Cooke 17729 (CAS); near Upton, Mount Shasta, 4000 ft., Hall & Babcock 4078 (UC); 1 mi. east of Highway 89–99 junction, Kuijt 1371 (UC); road to Gumboot Lake, south fork of Sacramento River, west of Shasta, 4500 ft., Smith & Bacigalupi (UC); west fork of Cottonwood Creek, Siskiyou Mountains, Wheeler 2783 (CAS, POM, LA); 2 mi. below Dry Lake Lookout, Oak Knoll Ranger Station, 5000 ft., Gill (FPA).

DISCUSSION. So much confusion existes as to this species in California that it is necessary first to make a few corrections.

To begin with, there is the question of Jepson's (1923) reference to Arceuthobium douglasii on Pseudotsuga macrocarpa (Vasey) Mayr in southern California. As far as I can discover there is no voucher for this suggestion in the Jepson Herbarium or in the University of California Herbarium at Berkeley, or elsewhere. In Jepson's field notebooks there is no mention of Arceuthobium douglasii. Whatever the statement was originally based on, at present the record is unacceptable.

A second source of confusion has been Jepson's (1914) misquotation of Engelmann (1880). In this work, Engelmann refers to A. douglasii var. abietinum Engelm. as occurring on Abies concolor (Gord. & Glend.) Lindl. ex Hildebr. in Sierra Valley, Sierra County. Jepson, however, simply repeats this locality for Arceuthobium douglasii, and this error is perpetuated by Gill (1935). The var. abietinum is undoubtedly referable to A. campylopodum, as are the early A. douglasii var. laricis and var. tsugense. There is no reliable record of A. douglasii (in the modern sense) from Sierra County.

A third error was first introduced by Jepson (1923) and again repeated by Gill (1935). It concerns a specimen collected by Mackie, "Lake Co., Aug. 1902, on *Pseudotsuga taxifolia*." Both Jepson and Gill refer to *Arceuthobium douglasii* in Lake County. Gill's reference is based on the Mackie collection, and Jepson's probably also. The specimen in question (UC 54672) includes some fragmented material, a couple of infected branches of *Abies* sp. [probably *A. grandis* (Dougl. ex Don) Lindl.], and a cone of *Pseudotsuga menziesii*. I have no doubt, both because of the flowering condition of the plants and because of their large size, that the collection is *Arceuthobium campylopodum*, and that the Douglas fir cone was included by mistake.

As it stands, then, A. douglasii is known only from the northern part of the state. In fact, the only known collection outside Siskiyou County was made within half a mile of the county line. There is in this species a most striking discrepancy between the geographic ranges of host and parasite. The common Douglas fir may be found in the Coast Ranges as far south as the Santa Lucia Mountains, and in the Sierra Nevada as far south as Big Creek (San Joaquin River), Fresno County. The dwarf mistletoe, almost exclusively restricted to this tree, somehow has not been able to invade large portions of its host's range. Whether these extensive areas of Douglas fir have remained healthy because of spatial isolation, resistance, or climatic barriers, or whether differences in forest composition here play

a decisive role in limiting the spread of A. douglasii, are questions which remain to be clarified.

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NUCLEAR CYTOLOGY OF THE CALIFORNIA MOUSE-TAILS $(MYO \\ \S URUS)^1$

DONALD E. STONE

Introduction

Published accounts of the chromosome numbers in the genus *Myosurus* are limited to three brief reports concerned exclusively with European representatives. In the 1945 edition of the "Chromosome Atlas," a single citation (Gregory, 1941) noted the chromosome number of *M. minimus* as n=8. A check of Gregory's paper, however, reveals that *Myosurus* was one of the few genera in the family for which he had no first hand information. Instead, his citation is based upon the work of Mann (1892) and Hocquette (1922), who found n=8 and 2n=16 respectively. The haploid number was published by Mann as a footnote to his figure 5: "Monaster stage of archesporium, with 8 chromatin segments." Hocquette's account was likewise lacking in details, as his study was part of a general survey of the Ranunculaceae.

The third reference to original work is in the 1955 edition of the "Chromosome Atlas." It is of interest to note that here the earlier citations of Mann and Hocquette are dropped in favor of a more recent

¹ Part of a dissertation submitted to the University of California at Berkeley as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

count by Ehrenberg (1945). Working on Swedish material, Ehrenberg found about 28 chromosomes in the somatic cells. His counts of nine cells showed variations of from 27 to 30 chromosomes, with the best three slides having 28, 28 and 29. He suggests that the Swedish material is tetraploid, being derived from a diploid race with a base number of 7. Hocquette's report of a haploid number of 8 is considered to offer little difficulty as the

TABLE 1. MYOSURUS SPECIMENS CYTOLOGICALLY EXAMINED AND DOCUMENTED.¹

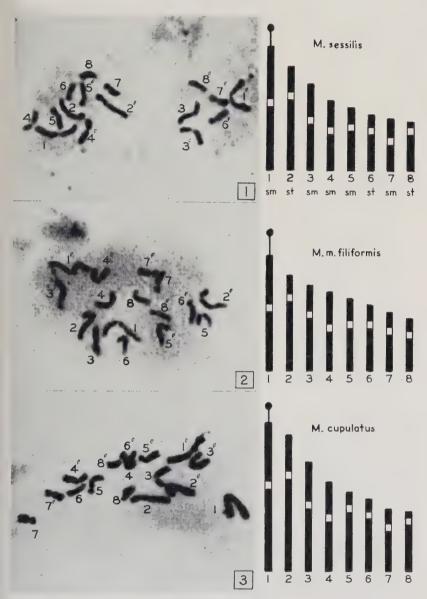
	Collection Data	N	2N	Fig.
<u></u>	sessilis Watson			
	Stone 1(14): 5 April 1953, 3 miles east			
	of Maxwell on the Maxwell Road, Colusa County.*		16	1
	Stone 1(10): same data as above.	8		4 & 5
M.	sessilis subsp. alopecuroides (Greene) Stone			
	Stone 7(22): 10 April 1953, same locality		16	_
	as above.	8		6 & 7
M.	minimus subsp. apus (Greene) Campbell			
	Stone 5(1): 10 April 1953, Manning Flat,			
	5½ miles west of Lower Lake on the road to			
	Kelseyville, Lake County	8		8
	Stone 5(2): same data as above.	8		9
	H. L. Mason 14275(2): 26 April 1952, 5 miles			
	northeast of Crows Landing on the Crows Landing			
	Road, Stanislaus County.		16	
M.	minimus L.			
	J. Lid, Stone 73(1): 21 June 1955, Hud Island			
	Vestfold County, Norway.		16	11
	Stone 3(5): 4 April 1953, Manning Flat, 5½ miles			
	west of Lower Lake on the road to Kelseyville,			
	Lake County.	8		10
	H. L. Mason 14501(4): 2 April 1953, 3 miles east			
	of Hanford on the road to Visalia, Kings County.	8		-
М.	minimus var. filiformis Greene			
	Stone 7(13): 10 April 1953, 3 miles east of Maxwell			
	on the Maxwell Road, Colusa County.		16	2
	Stone 9(2): Spring, 1953, Ajax Field in Willows,			
	Glenn County.	8		12-14
M.	aristatus subsp. montanus (Campbell) Stone			
	R. Bacigalupi 4238, Stone 15(5): April, 1953,		16	
	Big Bear Lake, San Bernardino County.	8		15
Μ.				20
	T. Robbins 3480, Stone 17 (1): 29 April 1952,	8		16
	Providence Mountains, San Bernardino County.		16	3

¹ Specimens documenting the chromosome counts have been deposited in the Herbarium of the University of California at Berkeley.

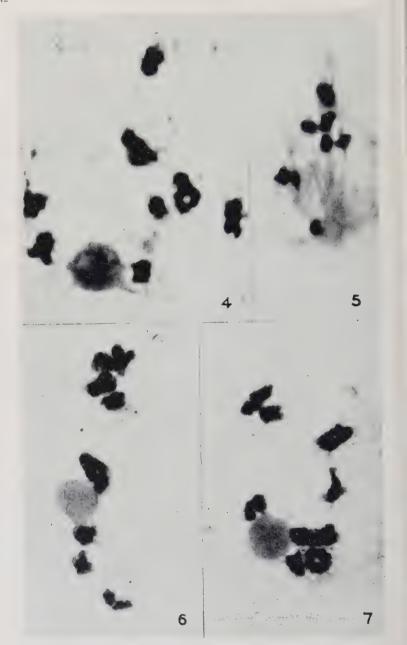
closely related genus of *Ranunculus*, which like *Myosurus* has large-Ranunculus-type chromosomes (Langlet, 1932), ranges from n=7, n=8 to n=64 (Darlington and Ammal, 1955).

When the problem of the existence of sympatric biotypes was first suggested (Stone, 1959), it was hoped that cytology might provide some

^{*} All localities are in California unless otherwise noted.



Figs. 1-3. Somatic metaphase chromosomes and idiograms of three *Myosurus* species: 1, *M. sessilis*, shoot-apex squash, × 2000; 2, *M. minimus* var. *filiformis*, root-tip squash, × 2200; 3, *M. cupulatus*, root-tip squash, × 1360.



Figs. 4–7. Meiotic configurations of M. sessilis and subspecies: 4, M. sessilis, diakinesis, \times 1850; 5, M. sessilis, metaphase I, \times 1850; 6 and 7, M. sessilis subsp. alopecuroides, diakinesis, \times 1850.

clue to the mechanisms involved in isolation. This hope, unfortunately, was not realized. A survey of chromosome numbers in nine heterogeneous California valley populations (Mason, 1957; Stone, 1957), representatives of two high-mountain species, and a collection from Norway, however, showed only diploid plants with n = 8 and 2n = 16. Although no deviations from the basic number of 8 were found, it is possible that specialized biotypes found in disjunct pools throughout California might prove to be exceptions. Additional information was sought in a karyotype study of three of the most extreme morphological types (figs. 1, 2 and 3). Here again, no differences could be established.

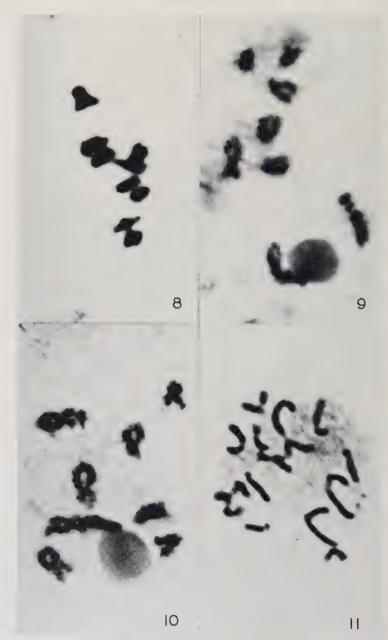
MATERIAL AND METHODS

All of the material examined cytologically was grown in the Botany Department greenhouse, University of California, Berkeley.

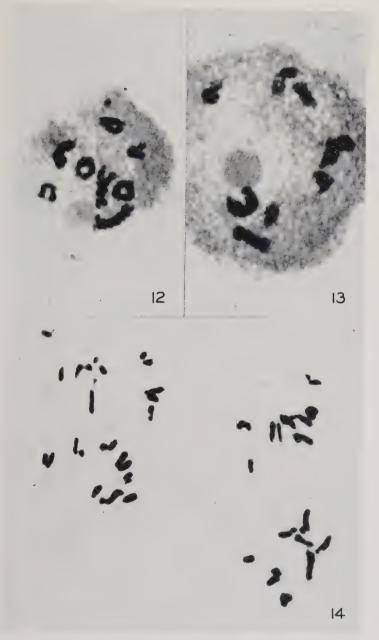
Mitotic stages were most readily obtained from the root tips of young seedlings or from the embryonic tissues of leaf bases and shoot apices. Fixation with acetic-alcohol (1:3) and staining with iron aceto-carmine proved satisfactory in root-tip squashes of young seedlings. Root tips of more mature individuals, however, were extremely difficult to squash, hence special techniques were found necessary. The following four-step process worked well on material examined immediately after squashing: (1) fixation of root tips in acetic-alcohol for 24 hours; (2) pre-staining of the material in aceto-carmine at 60° C, for 2 hours: (3) hydrolyzing in 1N HCl at 60° C. for 1 hour; and (4) washing in distilled water for 15 minutes, after which the material was stored in 70 per cent ethanol. Processed root tips were then squashed using additional iron aceto-carmine stain. Cells hydrolyzed in such a manner have light-stained nucleoli and dark stained chromosomes, and thus are quite favorable for observation of chromosome-nucleolar associations in mitotic prophase. Apparently there is a differential reduction of acidity in the pre-stained nucleus during the hydrolysis (Rattenbury, 1952). Due to the obvious difficulty of chromosome distortion in squashes, paraffin-section methods were tried. However, the minute size of the secondary roots (0.1-0.2 mm, in diameter) and the restricted meristematic region made sectioning efforts fruitless.

Stages of microsporogenesis were used in the study of the meiotic chromosome behavior. When obtained, active pollen mother cells were extremely useful in determining chromosome number, size, and pairing relationships. Three features affecting satisfactory results should be noted: (1) the period of active microsporogenesis; (2) the position of the bud; and (3) the size of the bud and stamens.

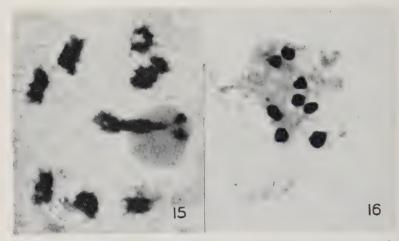
The period of microsporogenesis was found to be of extremely short duration. Out of a total of four or five young buds on a plant it was common to find that most had already matured, while the remainder were premeiotic. Possibly, poor greenhouse conditions were responsible for the shortened meiotic period, but judging from the luxuriant specimens, this



Figs. 8-11. Meiotic and mitotic configurations of M, minimus and subspecies: 8, M, minimus subsp. apus, metaphase I, \times 1850; 9, M, minimus subsp. apus, diakinesis, \times 1850; 10, M, minimus, diakinesis, \times 1850; 11, M, minimus, mitotic metaphase, \times 2800.



Figs. 12–14. Meiosis in M. minimus var. filiformis: 12–13, diakinesis, \times 1850; 14, anaphase II, \times 1500.



Figs. 15-16. Meiosis in two montane species of Myosurus: 15, M. aristatus subsp. montanus, diakinesis showing attachment of chromosome No. 1 (large satellited one) with nucleolus, \times 2000; 16, M. cupulatus, metaphase I, \times 2000.

does not seem likely to be the case. Perhaps a condition such as this, where meiosis occurs at a very early stage and over a short period of time, has a selective advantage in plants that survive in ephemeral environments such as vernal pools.

In all biotypes of *Myosurus* examined, meiosis occurs before peduncle elongation takes place. The meiotic buds are found buried deep in the basal rosette of leaves and peduncles of the more mature flowers. Meiotic buds are usually less than 1.5 mm. in length and hence are extremely difficult to find and remove. Killing and fixing of the entire plant, however. was found practical. Buds were removed under a dissecting microscope at $30\times$, and flower dissection was completed at $60\times$, with one stamen (anthers 0.3-0.5 mm. long) at a time being removed for squashing. Plants used for meiotic studies were fixed either in acetic-alcohol or in Linnert's fixative.

The photomicrographs in the accompanying figures were made using a Bausch and Lomb compound microscope having either a $90 \times (N.A. 1.30)$ or a $60 \times (N.A. 1.40)$ apochromatic objective and a $15 \times compensating$ eyepiece. The magnification of each figure is noted in the legend of the figure.

RESULTS

Mitotic Chromosome Number and Morphology

Detailed cytological studies were limited to the Manning Flat, Maxwell, and Willows populations (Table 1), but a survey of additional biotypes from the other California Valley populations established a single chromosome number of 2n=16. The photographs of figures 1-3, and 11, are representative of the mitotic squashes that were observed in this study. The

generic karyotype consists of 5 submedian and 3 subterminal chromosomes. The largest of the set bears a conspicuous satellite. The idiograms are based on the average of the homologous pairs of chromosomes, as measured in the corresponding photographs. The arbitrary classification of the centromere is based on the relative length of the two arms (Goodspeed, 1945); median (m), arm ratio 1:1; submedian (sm), arm ratio greater than 1:1 but less than 3:1; subterminal (st), arm ratio 3:1 or greater. It is quite apparent that although the satellited chromosome fits in the submedian class, it is very close to the median class, and for all practical purposes it can be considered as such. The conspicuous uniformity in the size gradient from the large satellited chromosome to the smallest subterminal chromosome is common to all three taxa. The most notable difference between the idiograms is the absolute size of the chromosomes. For example, the satellited chromosome is about 6 microns in figure 1, 6 microns in figure 2, and 7 microns in figure 3. As cell size and chromosome size are more or less interdependent and seem to fluctuate considerably in the same plant, no significance was attached to the slight differences in length.

Examination of Norwegian material (fig. 11) has proven the chromosome number to be identical to that of California specimens. Ehrenberg's polyploid counts still remain to be verified.

Meiotic Chromosome Number and Pairing Relationships

Diakinesis (figs. 4, 6, 7, 9, 10, 12, 13, and 15) was by far the most common meiotic stage encountered. In part, this occurrence might be attributed to the selected time of fixation: it was found that best results were obtained if fixation was limited to the time between 12 noon and 2 p.m. Infrequently, metaphase I stages (figs. 5, 8, and 16) were found. Later stages in the meiotic sequence were so rare that only two pollen mother cells were observed in the anaphase II stage (fig. 14). The second meiotic anaphase is frequently useful in denoting karyotype differences (Chambers, 1955) and in the case of figure 14 it is possible to verify centromere positions established in mitotic preparations. All of the figures show 8 pairs of chromosomes with no indication of pairing difficulties. It is of interest to note the association of the large satellited chromosome (No. 1) with the nucleolus in the diakinesis figures.

SUMMARY

Mitotic and meiotic chromosome counts have been made for each of seven taxa of *Myosurus*, on six of which no counts have previously been reported. All examined specimens of the genus *Myosurus* displayed a diploid number of 16, and a haploid number of 8 chromosomes, with no meiotic irregularities.

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VARIATION IN SECTION TRIGONOPHYLLAE OF NICOTIANA

PHILIP V. WELLS

Section Trigonophyllae of the genus *Nicotiana* is peculiar to the warm deserts of southwestern North America, and ranges from California to Texas and southward locally as far as Oaxaca. The section, as defined by Goodspeed (1954), includes two species: *N. trigonophylla* Dunal, the range of which coincides with that of the section, and *N. Palmeri* Gray, which is apparently found only in southwestern Utah and western Arizona.

During the course of an ecological investigation of N. trigonophylla throughout its range in the United States, the writer encountered facts which cast doubt on the validity of the specific rank of the taxon N. Palmeri.

The two members of the section Trigonophyllae are segregated as follows by Goodspeed (1954) in his key and text:

Calyx 8–11 mm. long; corolla 12–23 mm. long, limb 3–4 mm. wide, erect in bud; seed ca. 0.5 mm. long; cauline leaves obtuse to acuminate....*N. trigonophylla* Calyx 15–17 mm. long; corolla 23–32 mm. long, limb 5–6 mm. wide, oblique in bud; seed ca. 0.7 mm. long; cauline leaves acute to acuminate......*N. Palmeri*

Both taxa have the same chromosome number (12 pairs) and Kostoff (1943) reported that F_1 hybrids between the two show twelve homologous pairs of chromosomes at meiosis.

The writer visited several of the major herbaria¹ of the United States and examined the collections of *Nicotiana*, section Trigonophyllae. Only

nine collection numbers were encountered which were labelled or annotated as N. Palmeri. Of these, one was an intermediate mentioned by Goodspeed (1954), and of the remaining eight specimens only two possessed corollas appreciable larger than those of N. trigonophylla: 1) Keck 4255 (UC) Gillespie Dam, Maricopa County, Arizona, March 22, 1936. "In lava rock at cliff base." 2) Gould 1611 (NY) St. George, Washington County, Utah, April 20, 1942. "Southern slope of Black Hill... on rock ledges and among volcanic boulders." Both of these specimens have corollas more than 30 mm. in length. This is larger than the type collection (Palmer 433), which is intermediate between these extremes and N. trigonophylla.

In the herbarium at Dixie College at St. George, Utah, there were seven collections of section Trigonophyllae from the basalt-capped mesa just west of St. George (the site of *Gould 1611*). Of these, only one was labelled *N. Palmeri*; the other six (including one determined by I. Tidestrom) were labelled *N. trigonophylla*. None were more than intermediate between the two taxa. On the other hand, the writer has grown plants from seed collected from this same site which produced corollas 27 mm. in length, which is within the size range for the flowers of *N. Palmeri*.

Specimens and seed were collected over a large part of the range of section Trigonophyllae in the United States. Measurements of various taxonomic characters were made both on collected plants and on plants grown from seed in the greenhouse. The results are presented in Table 1, where a number of size classes are established for each character investigated. The number of measurements falling within each size class is given, thus illustrating the modal class and the range of variation. For the greenhouse-grown plants each figure represents the number of plants having that particular mean character size, while for the collected specimens, each figure indicates the number of measurements falling in a size class.

The populations investigated show a trend toward *N. Palmeri* characters as one approaches the Washington County, Utah area. Whether one regards *N. Palmeri* as a distinct species or prefers to sink it to the subspecific or varietal level, it is apparent that the two taxa are not clearly delineated, but intergrade with respect to all characters measured. This morphological intergradation is probably best interpreted in a topoclinal sense, since no ecological gradients appear to be involved. In the range of *N. Palmeri*, section Trigonophyllae occupies its three usual ecological niches: 1) bedrock outcrops and talus; 2) dry washes; 3) ruderal sites (roadsides, etc.), but it is most prevalent in the first mentioned (Wells, 1959).

¹ The following institutions were visited: Bureau of Plant Industry (Beltsville, Md., Missouri Botanical Garden, St. Louis, New York Botanical Garden, Rancho Santa Ana Botanical Garden, Claremont, California, University of California, Berkeley, and the United States National Herbarium, Washington, D.C.

TABLE 1. VARIATION IN TAXONOMIC CHARACTERS IN SECTION TRICONOPHYLLAE OF Vicotiana IN DIFFERENT PARTS OF ITS RANGE

Localities (by County)) Length of Corolla (excluding limb), mm.	gth o	of Co	rolla	(ехс	ludin	ng lin	ıb),	nm.		2	Ä	ength	m. Length of Calyx, mm.	alyx	mm ,				T	Total Limb Width, mm.	Cimb	Widt	h, m	n.		Lim	Limb Lobe Width, mm.
	16 17 18	- 1	19 20		21 22	2	3 24	2.5	23 24 25 26 27	27	00	6	9 10 11	11	12	13	13 14 15		9	0 1	9 10 11 12 13 14 15 16 17	13	14	15	16		3 4	10
Kimble, Texas	3 1 1										-	2	2						2	7	_						. 3	
Pima, Arizona	2 3		2	_							-	4	~ -		-	-				7	4	,					no n	C
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Washington I'tah	4			,	4	(~)										. ~	-					-	4	-		4	2	7
Washington, Utah								4	3						_	~	~	7				2	7	7				9
										0	OLLE	CTED	SPEC	COLLECTED SPECIMENS	v. 7													
				16 1	Le ₁	ength 18	of P	Periant 20 2	Length of Perianth (excluding limb), mm. 18 19 20 21 22 23 24 25 26	rcludin 2 23	ing lin 3 24	imb),	, mm.	5 27		30	00	Leng	ength of	of Caly	Length of Calyx, mm. 10 11 12 13 14	nm. 14	15		0.5	Length 0.5 0.6	of Se 0.7	Length of Seed, mm. 5 0.6 0.7 0.8 0.9
			1													•							1		1			
San Bernardino, California	rnia			-													_											
Riverside, California																			_									
Culberson, Texas					_												_									L/S	S	
Eddy, New Mexico				7		3											2	-	2							7	3	
Pima, Arizona						2													2							3	7	
Pinal, Arizona						2												_							_	6		
Kimble, Texas						4	3										-	2	_							poid	-1	2
Brewster, Texas																			2							3	9	-
Pima, Arizona																	_	_								00	-	
Cochise, Arizona					_	2		-											2							3	- 1	
Brewster, Texas				posel		2		7										2	4							9	4	
Clark, Nevada					_			7	****										7							12	15	~
Washington, Utah								2												_	_						4	9
Clark, Nevada								7	_		seed.								3	_						18	1.2	
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The tendency of plants of section Trigonophyllae to occur in small, isolated populations, and the localization of plants showing N. Palmeri characters in certain northwestern portions of the range of the section, suggest the operation of the Sewall Wright effect in bringing about differentiation. A related possibility is the selection of larger flowers by some local pollinator in the N. Palmeri range.

The taxon N. trigonophylla Dun. is acknowledged by Goodspeed (1954) to be a variable one. With respect to the validity of N. Palmeri, Goodspeed (1945) wrote: "...N. Palmeri is morphologically so closely related to N. trigonophylla as doubtfully to deserve specific recognition ...". In his 1954 monograph, he wrote: "This species (N. Palmeri) is obviously close to N. trigonophylla. It is distinguishable even from large flowered races of the latter by the greater coarseness throughout, by longer corolla, and by broader, whiter, more horizontal limb with lobes at times slightly concave. Maguire and Blood 1456, 15 miles SW of Leeds (Washington Co.), Utah (UC) is an example of an intermediate between the two."

In the herbarium of the New York Botanical Garden, there is a series of collections of section Trigonophyllae from Sonora and Baja California. On one of the herbarium sheets (MacDougal 41), there are some remarks by a reviewer of these collections (unsigned). In summary, he finds the material "not uniform but contains 2 forms with very different pubescence. One is densely glandular villous-tomentose and is so oily as to heavily stain collecting paper. The two forms deserve nomenclatural recognition, but at present it seems impossible to determine which is typical form. N. Palmeri Gray of Arizona seems intermediate in its characters, but nearest to eglandulose form." The writer also found wide variation in several characters (including flower size) in the Mexican collections of section Trigonophyllae. It seems likely that an intensive study of the N. trigonophylla complex in Mexico might uncover variants at least as divergent as the currently accepted N. Palmeri.

Considering the variability of N. trigonophylla and the continuous intergradation between it and N. Palmeri, and also the very meager representation of the latter taxon in herbaria, it does not seem too conservative to relegate N. Palmeri to subspecific or varietal status. This, in fact, has already been done by Marcus E. Jones (1908) who reduced N. Palmeri Gray to N. trigonophylla Dun. var. Palmeri (Gray) Jones.

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STUDIES ON SECOTIACEOUS FUNGI VII. SECOTIUM AND NEOSECOTIUM.

ROLF SINGER AND ALEXANDER H. SMITH¹

We have had occasion to mention the genus *Secotium* in the narrower sense as based on *Secotium gueinzii* Kunze from South Africa. These references to *S. gueinzii* in the preceding parts of our studies on secotiaceous fungi were motivated by the necessity of comparing the characters of the type species of the genus with the characters of the other genera of the family as proposed in our previous papers.

We have now arrived at the question: what is the position of Secotium

gueinzii, and which other species of Secotium are close to it?

In the first place we wish to redescribe the species to facilitate the comparison.

SECOTIUM Kunze, Flora 23:321. 1840.

SECOTIUM GUEINZII Kunze, 1.c. p. 322.

Gastrocarp convex, truncate below or not, always deeply sinuate underneath along the apex of the stipe (like *Endoptychum depressum*), semiglobose to campanulate, 30–60 mm. broad, about 32–42 mm. tall.

Peridium (inner) tessellate (with canal-like depressions), not gelatinized, white-buff (dried fuscidulous-yellowish), sometimes covering the gleba completely, sometimes pulled back (down) to expose some part of gleba; gleba loculate, with small chambers which do not show lamellar arrangement in any form but are winding, irregular, and unequal, not pulverulent, the walls white, thin, ochraceous buff to light brownish and said to have been pale olive, the exposed surface of gleba (if any) vertically surrounding the apex of the stipe.

Stipe up to 70 mm. long and 5–10 mm. broad at apex, up to 22 mm. broad at base, buffish colored, apparently smooth and glabrous, dry, stuffed; columella continuous with the stipe and either percurrent or not, if not, then sending out tramal plates with thick branches which merge with the normal thin tramal plates making up the loculi, at times changing direction in relation to the stipe and becoming oblique rather than vertical, broadened into the upper portion of the peridium if percurrent, white; volva said to be present, whitish, eventually disappearing except at the base of the stipe where it appears cothurnate, a distinct annular veil such as seen in *Endoptychum depressum* not described, not seen in the fragments available, and not clearly shown in illustrations. Context white, dry-fleshy, probably when fresh somewhat like *Endoptychum agaricoides*.

Spores (8.5–) $11-14 \times (6.3-)$ 8.2–9.7 μ , short ellipsoid but ovate in frontal view, somewhat inequilateral in profile (asymmetric), with oblique eccentric sterigmal appendage, pale olive-melleous to melleous-

¹ Papers from the University of Michigan Herbarium and the Department of Botany, No. 1087, University of Michigan, Ann Arbor, Michigan.

hyaline, the wall thick and complex (at least four wall-layers discernible), smooth, some with an apical germ pore, or some with an apical truncation but without a demonstrable discontinuity in the wall (or else pore incomplete and spore not truncate), slightly metachromatic in cresyl blue but absorption of the cresyl blue very variable, if weakly stained, a lilac line along the endosporium visible and inner two layers sometimes remaining incolorous, when strongly stained the whole wall and interior deep blue as in spores of *Chlorophyllum molybdites*, correspondingly, with Melzer's reagent distinctly pseudoamyloid but some remaining inamyloid and a few discoloring only partly; not forming a pulverulent mass in the gleba.

Basidia about $28 \times 9.7\mu$, 4-spored, sterigmata variable, some thin and straight but oblique, some thin and slightly curved (somewhat intermediate between "agaricoid" and "gastroid"); cystidia not seen, but yellow "Pollinarien" described and illustrated by Corda.

Trama hyphous throughout, in places very slightly gelatinized, hyaline, in peridium extremely irregular but more radially arranged in outermost layer of endoperidium, the hyphae of all layers $2-6~\mu$ in diam., inamyloid and with clamp connections.

Terrestrial on the sand steppes of the Cape of Good Hope, South Africa, Uitenhage, fruiting in summer (December). Leg. *Queinzius*, comm. M. C. Cooke (NY, part of type).

Another part of the type is at Kew (Singer has seen but not studied it, but he is certain that it is part of the same collection, which is corroborated by the fact that what little Heim communicates about the "Berkeley-type" coincides well with our findings). It is possible that part of this was also in Corda's Herbarium which is in Prague.

This species has the same essential spore-wall characters as *Endoptychum agaricoides* and *E. arizonicum*, namely the pseudoamyloid reaction, the thick, many-layered wall, and the relatively light color (varying to hyaline). In spite of these similarities, there are important differences such as the presence of a volva, non-pulverulent gleba, abundant clamp connections, and large ellipsoid spores with a germ pore. In view of these differences it appears illogical to us to place *S. gueinzii* in the same genus with *Endoptychum*. This was apparently also Zeller's point of view.

However, two other species, intermediate in their characters, need to be considered here. One is Secotium macrosporum Lloyd. It is intermediate in such basic characters as the pulverulent gleba and degree to which clamps are present, but is strikingly distinct because of the complex ornamentation of the spores. With some modifications the spore ornamentation is the type that is found in some tropical Lepiotas (Leucoagaricus) and/or (this is significant), in the Lycoperdaceae. We shall discuss the affinities of this interesting species later, but considering its differences from both Endoptychum and Secotium, we cannot convince ourselves that according to any generic concept short of re-establishing Secotium sensu lato, can S. macrosporum be considered congeneric with either Secotium or Endoptychum.

This establishes *Secotium* as a monotypic genus, and necessitates establishing a new genus for *S. macrosporum*. We propose for it the new generic name *Neosecotium*, this being a New World *Secotium* and a species only now critically analyzed (Neo—new; secotium—a loculate system).

Neosecotium gen nov.

Carpophoris haud volvatis, pallidis, stipitatis, columella percurrente; gleba demum paulum vel manifeste pulveracea; sporis hyalinis leviter ochrascentibus, pseudoamyloideis, poro germinativo instructis, globosis, membrana admodum crassa reticulatim fracta ornamentatis; fibulis praesentibus sed sparsis.

Typus generis: Secotium macrosporum Lloyd.

Neosecotium macrosporum (Lloyd) Sing. & Smith, comb. nov. Secotium macrosporum Lloyd, Mycol. Writ. 1:139. 1903.

Gastrocary 1-3 cm. high and 1-2 cm. thick, subelliptic to nearly

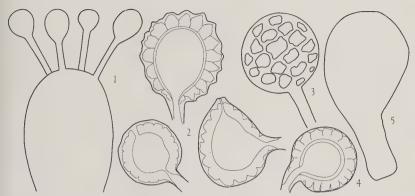
globose, the margin not separating from the stipe-columella.

Peridium smooth, avellaneous or paler, the lower portion whitish-pallid at times.

Gleba chambered at first, but somewhat pulverulent and at maturity little if any structure visible, in immature stages showing chambers oriented in an obscure lamellar orientation, about wood brown (R) near maturity or finally becoming more cinnamon, not separated from columella.

Stipe-columella percurrent, pallid throughout as dried, 2–3.5 mm. diam. in widest place (as dried), very little (2–3 mm.) projecting below the gastrocarp as a stipe.

Spores globose and 13.5–18 μ or 14–18 imes 12–15 μ and subglobose to slightly ovate, ochraceous to tawny in KOH (depending on degree of maturity), dark red-brown in Melzer's solution (pseudoamyloid), with a short to rather long sterigmal appendage as in many Lycoperdaceae, the pedicel hyaline and thin-walled except for the area where the thickening of the spore wall projects down into it slightly, centrally attached or rarely slightly eccentric; spore wall complex, at maturity with a thin hyaline perisporium which adapts itself to the configuration of the wall beneath (exosporium and possibly endosporium combined); exosporium and endosporium together 3-5 µ thick, rusty brown in KOH at maturity but nearly hyaline earlier, deep red-brown in Melzer's solution, smooth at first but soon becoming cracked into an areolate pattern and the fissures gradually deepening to produce a warty to almost echinulate effect and at this time the spore surface appearing distinctly roughened, but perisporial membrane still visible over warts and depressed into the crevices, in young stages where the inner thick wall is still hyaline an apical germ pore can be observed in some spores, and in abnormal spores a lateral beak furnished with a distinct pore is clearly evident, the pore obscured in old spores by the cracking up of the thick inner layer of the wall.



Figs. 1–5. Neosecotium macrosporium: 1, upper part of basidium showing tubular sterigmata and young spores, \times 450; 2, mature spores in optical section, \times 1000; 3, surface view of nearly mature spores, \times 1000; 4, optical section of immature spores, \times 1000; 5, young basidium, \times 450.

Basidia large, $25\text{--}37 \times 14\text{--}17.5\,\mu$, clavate to subelliptic-pedicellate, thin-walled and hyaline or the wall slightly thickened and brownish—hence the cell more persistent than usual; sterigmata typically 4 and tubular, not often tapering appreciably and the young spore acropetally attached or very rarely appearing slightly eccentric. Cystidia, none observed.

Subhymenium of broad intricately interwoven hyphae, hence in section appearing somewhat cellular from cut hyphal ends; hyphae of the peridium filamentous, many hyphal cells somewhat to markedly inflated (4–12–18 μ in diam.), the outer layer more or less radially arranged and melleous to dingy ochraceous in KOH, gradually paler toward gleba, not at all gelatinous or toward gleba only sub- gelatinous (slightly translucent in KOH); clamp connections absent to rarely present.

The type was collected near Dallas, Texas, by E. P. Ely. The best material we have seen, however, is a collection by R. Sprague, June 13, 1941, in grass plots on sandy soil at Mandan, North Dakota (NY).

This is a most interesting species in many respects: the long, tubular sterigmata which often break off leaving the upper half attached to the spore as a pedicel or appendage, the tendency of the gleba to become powdery at maturity, and the type of spore ornamentation in mature spores are all strongly reminiscent of the Lycoperdaceae, so much so, in fact, that we are inclined to believe that N. macrosporum actually does represent a true link connecting the Secotiaceae to that group. The outer surface of the dried peridium is almost Calvatia-like in texture, but this, of course, may not have any phylogenetic significance beyond that indicated by the type and arrangement of the hyphae of the outer zone of the peridium.

The pallid to avellaneous tone of the mature gastrocarp and its texture are also reminiscent of *Lepiota naucina*. Actually, aside from the shape

of the spore and the peculiar way in which the inner wall layers break up, the spores themselves show resemblances to those of *Macrolepiota* and *Leucoagaricus* by the presence of a germ pore (though it is obscured at maturity) and the strong pseudoamyloid reaction of the thick inner wall. Also the spores are metachromatic in Cresyl blue—at least the pale colored spores are. These characters appear to us to connect *Neosecotium macrosporum* to the Agaricales, family Agaricaceae sensu Singer, and very likely in the vicinity of *Chlorophyllum* and *Macrolepiota*. Hence we have here a connecting link, as we see it, between the Lycoperdaceae on the one hand and a family of agarics on the other.

As far as we are aware, this is a heretofore unsuspected connection between the two groups, and when viewed in this way it is cause for much interesting speculation on the course which evolution has followed. Since in this series of papers we are not discussing the direction of evolution, we shall limit ourselves to considerations which we believe to be based on facts as follows:

The lycoperdaceous fungi show a wide range of spore color just as does the family Agaricaceae, and, though the spores in the Lycoperdaceae are small, many show a sufficiently similar type of ornamentation to make it imperative that spore structure in that order now be studied by the techniques in use for the study of spores in the Agaricales.

The problem of the powdery gleba in the Lycoperdaceae is now no problem at all as far as its being an obstacle to ascertaining connections to the Agaricales. In a number of species of Agaricus the gills become very soft and almost collapse after maturity, and in carpophores which did not open but which dried out *in situ* it is a simple matter to understand how these structures could break down to a powdery consistency. The presence of a highly developed capillitium is certainly to be regarded as an advanced character in the Lycoperdaceae, but this, no matter from which source one derives the Lycoperdaceae—the agarics or lower Gastromycetes—does not offer any serious hurdle to establishing relationships in either direction. Any hymenophoral trama with thick-walled hyphae could easily give rise to "capillitium" if the remaining trama consisted of thin-walled perishable hyphae. There is no reason why thickwalled hyphae should not appear "de nova" in the glebal trama of Gastromycetes in more than one evolutionary series, since wall-thickenings of hyphae are one of the commonest types of hyphal adaptation in the fungi as a whole.

The second species of *Neosecotium* was found among the collections of *Arcangelliella* in the Zeller Herbarium. A redescription of it follows:

Neosecotium africanum (Lloyd) comb. nov. Octaviania africana Lloyd, Myc. Writings 7:1142. 1922. Octaviania africana Verwoerd, S. Afr. Journ. Sci. 22:164. 1925. Arcangeliella africana (Lloyd) Zeller & Dodge, Ann. Mo. Bot. 22:365. 1935.

Fructifications spherical, 10-15 mm. thick, drying cinnamon-brown to

Table 1. Comparative Features Indicating Intermediate Position of Neosecotium macrosporum between Endoptychum arizonicum and Secotium gueinzii.

	Endoptychum arizonicum	Neosecotium macrosporum (Secotium macrosporum)	Secotium gueinzii
SEPTA	without clamp connections	some with, some without clamps	with clamp connections
Volva	none	none	present
PERIDIAL SURFACE	rough but not tessellate	smooth	tesselate
GLEBA	pulverulent (strongly)	pulverulent (moderately)	non-pulverulent
SPORES			
ORNAMENT	smooth	ornamented	smooth
SIZE	small	large	large
SHAPE	subglobose	globose	ellipsoid
PORE	none	present	present

Dresden brown; peridium hard, duplex, the outer layer 140–160 μ thick, composed of closely woven slender, hyaline hyphae 1.5–2 μ in diam., the inner layer 375–400 μ thick, composed of hyaline, more loosely woven septate hyphae 3–4 μ in diam., "with lactiferous ducts" . . . Zeller & Dodge, separable; gleba drying from ferruginous to snuff brown; tramal plates 15–30 μ thick; basidia clavate, 23–30 \times 7–8 μ , sterigmata 10–15 μ long and filiform.

Spores (giant spores) 17–20 \times 14–16 μ , "normal" spores 13–15 \times 10–13 μ , subglobose to broadly ellipsoid; sterigmal appendage pedicellate; dingy yellowish in KOH, *dark red-brown* in Melzer's reagent (pseudoamyloid); ornamented and thick-walled, inner wall about 2 μ thick, outer wall broken up into a pattern of broad obtuse to flattened warts due to the cracking of the wall; no germ pore found.

The description of the spores was taken from the part of the type in the Zeller Collections of the New York Botanical Garden. The hymenium and tissues of the fruiting body failed to revive sufficiently for critical study. It is more than evident to us that because of the pseudoamyloid spores with their characteristic ornamentation the species belongs in Neosecotium even though in the material available we failed to establish the presence of a germ pore. The hard, brown peridium should amply distinguish N. africanum from N. macrosporum. From what we were able to ascertain from the limited material available, it appears to us that N. africanum is more gastroid than N. macrosporum, in fact may represent a distinct genus at the level of Martellia. Because it represents a different level of evolution, it is not included in the chart with the other distinctly secotiaceous species.

Naturally, the genera *Endoptychum*, *Neosecotium*, and *Secotium* form a definitely circumscribed and sharply outlined group—a tribus or sub-

family-which may also contain such genera as Polyplocium Berk., Gyro-

phrangmium Mont., and Longula Zeller.

Since we do not wish to enter such intricate questions of purely gastromycete taxonomy as the possibility of maintaining all three last-named genera (which seem to us extremely close to each other), and since our experience with them is relatively limited, we prefer to omit these genera for the time being. However, their close relationship to Secotium sensu stricto as well as Endoptychum cannot be overlooked.

REVIEW

Comparative Morphology of Vascular Plants. By Adriance S. Foster, and Ernest M. Gifford, Jr. 555 pp., 213 figs. W. H. Freeman, San Francisco. 1959. \$9.00.

The literature of vascular plant morphology has been greatly enriched by this new textbook by two prominent teachers and researchers at the University of California at Berkeley and Davis. In contrast with other morphology texts that have appeared in recent years, this is a product of men who have devoted their entire careers to the higher plants. As a result, the book is organized in a manner that emphasizes morphological problems of current interest in this area, with subdued treatment of the burning questions of morphology of the early years of this century that are currently only of historical interest. This book is likely to enjoy a long active life as a textbook and reference work, therefore a detailed review seems justified.

A unique feature that sets apart "Comparative Morphology" from earlier text-books is the organization of material into two sections. In the first part, consisting of six chapters, the principal characteristics of the vascular plants are surveyed in a comparative fashion; in the second part individual chapters are devoted to treatments of the plant groups in systematic sequence. The classification system of Tippo is followed throughout. Extinct groups are treated in an integrated manner alongside their living relatives, but the emphasis is on modern plant types. Detailed descriptive material is not presented for its own sake, but rather as evidence for morphological or phylogenetic conclusions. The detail might be described as interpretative and illustrative rather than as encyclopedic.

The opening chapter tells the beginning student what morphology is all about. There is a discussion of the concept of homology, and of the kinds of morphological evidence that have proved most useful in reconstructing concepts of phylogeny, such as ontogeny, adult form, and the fossil record. The frontiers of modern experimental morphology and morphogenesis are described briefly and some pertinent unanswered questions are posed. The following chapter deals with the overall characteristics of the phylum of vascular plants, giving an outline of a typical life cycle involving an alternation of generations. The existence of apospory and apogamy and the significance of these phenomena on the classical theories regarding the origin of alternate generations is discussed. The phylum is then divided into the usual four subphyla of Eames and Tippo.

Four chapters dealing with the principal areas of morphological investigation are devoted to the vegetative sporophyte, the sporangia, the gametangia, and to embryogeny. Under the heading of vegetative sporophyte are included discussions of the general structure of shoot and root, types of branching, types of leaves, microphylls versus megaphylls, and the phylogenetic origin of leaves according to Bower. The Telome Theory is presented briefly. The area of plant anatomy is entered with a discussion of the problems of classification of tissues and tissue systems. The system of Sachs is presented, and the structure and development of the principal tissues are

described. The chapter closes with a résumé of the historically important Stelar Theory. In this section the uses of the terms dictyostele and eustele are clarified.

The chapter on sporangia describes their function, position, and the organization of sporophylls into strobili in some groups. The structure and development of the two types of sporangia, the eusporangium and the leptosporangium are described, with an excellent series of comparative developmental drawings. The phylogenetic significance of the presence of two sporangium types is discussed. The following chapter on gametangia contrasts antheridia with archegonia in development, structure, and position. The concluding chapter in the first section of the book deals with embryogeny; the parts of embryos, polarity, and the development of the embryo from the zygote. The phylogenetic aspects of the study of embryo development are discussed.

The second section of the book opens with three chapters dealing with the subphyla usually known as the lower vascular plants. The Psilopsida are introduced with an historical treatment of their discovery, followed by synopsis of their classification into two orders and three families, Rhynia, Horneophyton, and Asteroxylon are described. Treatment of these fossils is limited to their general organography and anatomy. Psilotum and Tmesipteris are covered in much greater detail. Included in the description of the sporophyte structure is a discussion of the interpretation of the nature of the stem appendages, and of the multilocular sporangia found in these genera. The gametophyte generation is discussed in greater detail than is usual in recent texts, incorporating the results of contemporary workers like Bierhorst. The brief section on embryo development is followed by a concluding summary for the group. In the presentation of the details of structure and development of the sporangia, gametangia, and embryo, the earlier introductory chapters on these organs serve as a basis for comparison. In the usual treatment which lacks such introductory chapters, the organs of Psilotum must be studied by the beginning student, detached from the reality of the plant world that he knows.

The Lycopsida are treated in similar fashion, but here the living genera Lycopodium and Phylloglossum are described first, followed by the extinct Protolepidodendron and Baragwanathia. Then follow Selaginella, the Lepidodendrales, Isoetes, and the Pleuromeiales. Throughout this chapter much recent research is presented, along with the necessary details of structure and development that are part of the usual subject matter. The chapter on the Sphenopsida follows, using the same pattern of presentation. Equisetum is described first in detail, followed by a brief statement on

Hyenia. Sphenophyllum and Calamites conclude the subphylum.

The Pteropsida include the vast majority of living vascular plants and are described under a series of ten chapter headings. The first is a brief introductory description of the group, followed by another chapter which introduces the Filicinae. This chapter includes a very brief discussion of fossil fern foliage in general, and of the Coenopteridales in particular. The taxonomic summary for the ferns is included here, followed by a list of critical areas of morphological study compiled by Bower. The Eusporangiate Ferns and Leptosporangiate Ferns are treated next under separate headings. The latter group, which includes most living fern genera, is treated as a whole in great detail. Excellent series of drawings illustrate the degrees of compounding of fern fronds, variations in venation patterns, variation in sorus structure and position, the development of the sporangium, sporangium structure and various types of annuli, types of sorus in regard to order of maturation of the sporangia. The vast array of stele types found in the ferns is illustrated by an excellent series of photomicrographs. The gametophytes and embryos are described in the same manner as in the lower groups. A section dealing with special problems in fern morphology discusses "phyletic slide" and the relationship between sorus position and phylogeny. Recent work in experimental morphology of the ferns by Wardlaw and others is carefully reviewed. A brief résumé of the problems of fern systematics is included, illustrating the relationship between morphology and phylogeny, between phylogeny and classification. In the course of the systematic treatment, the principal families are briefly described, with fuller treatment of the Marsileaceae.

The Gymnosperms are covered by four chapters. The first is an introductory

conspectus of the group which includes brief treatments of the extinct orders Cycadofilicales, Cordaitales, and Bennettitales. The development and structure of the seed are covered here, including the details of ovule ontogeny, megasporogenesis, the formation of the megagametophyte, pollination, and fertilization. This discussion is followed by a brief statement on embryogeny and seed maturation. The second chapter in this series is devoted to the living cycads and Ginkgo. Megasporophyll evolution is illustrated by drawings of various cycads; the cycad life cycle by another series. The details of ovule development and of embryogeny not found in the introductory chapter are included here. The Coniferales occupy the third chapter and are introduced by a systematic treatment of the principal families. This is followed by the usual section on organography and anatomy. Florin's work on Paleozoic and Mesozoic conifers is reported in connection with leaf and strobilus evolution and structure. The life cycle of modern conifers is illustrated by Pinus. Included here are the details of fertilization, embryogeny and seed development. Then other conifers are compared with Pinus. The final chapter on the Gymnosperms deals with the Gnetales. The structure and life cycle of Ephedra are presented in detail, followed by a brief statement of the differences between Ephedra and the other genera, Gnetum and Welwitschia.

The final section of the book consists of two chapters on the Angiosperms. The first of these chapters treats the general structure and evolution of the group, while the second is devoted to the reproductive cycle. Under general structure, leaf morphology is described in detail, with series of illustrations of venation patterns. Stem and root structure are covered more briefly, but a concise statement of modern views on nodal anatomy and its phylogenetic significance is included, as is a brief statement on wood anatomy. The major part of the chapter is devoted to the problems of floral morphology, including theories of the nature of the flower, and the impact of evidence from floral vascular anatomy and from floral ontogeny on these theories. The vast body of work on primitive woody Ranales by Bailey and his associates during the past twenty years is drawn upon for evidence on phylogeny of stamens and carpels. The last chapter on angiosperm reproduction describes microsporangium development and microsporogenesis, the development of the male gametophyte, the ovule, megasporocyte, megasporogenesis, and embryo sac, with detailed discussion of the important types of the latter. The events of fertilization, endosperm development, and embryogeny follow, with a final discussion of seeds and seedlings.

In summary, Foster and Gifford's "Comparative Morphology of Vascular Plants" is an excellent work featuring clear discussions and illustrations, with an organization that should prove a boon to morphology teaching.—Sanford S. Tepfer, University

of Oregon, Eugene.

NOTES AND NEWS

From June through late December, 1959, with the aid of a National Science Foundation grant, Dr. Fritz Ehrendorfer intensified his field and laboratory studies, started several years ago, on the genus *Galium* in the western United States. He returned to Vienna to take up his new duties as Assistant Curator of the Naturhistorisches Museum.

PROFESSOR HERBERT L. MASON, who recently was the recipient of a Fulbright award, will be taking a sabbatical year from the University of California commencing February 1. He will be in residence at the University of Auckland, New Zealand, devoting his time mainly to studies of floristic relations in the Southern Hemisphere.